

## Diversity, structure and dynamics of a gallery forest in central Brazil

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### Abstract

The structure and dynamics of approximately 64 ha of undisturbed gallery forest were studied over six years. Trees from 31 cm gbh (*c.* 10 cm dbh) were measured every three years from 1985. They were in 151 (10×20 m) permanent plots in the Gama forest in the Federal District of Brazil. Natural regeneration (individuals under 31 cm gbh) was measured in subplots (of 2×2 m, 5×5 m and 10×10 m) within the 200 m<sup>2</sup> plots. The total tree flora (gbh ≥ 31 cm) consisted of 93 species, 81 genera and 44 families in 1985. The Leguminosae, Myrtaceae and Rubiaceae were the families richest in number of species. Most individuals and species were under 45 cm diameter and 20 m high while the maximum diameter per species ranged from 30 to 95 cm. The density structure of trees and natural regeneration was similar, in which the densities of *c.* 80% of the species represented less than 1% of the total density. The periodic mean annual diameter increment for trees from 10 cm dbh, was *c.* 0.25 cm/year. Variability was high with coefficients of variation *c.* 100% or more. The Gama community may maintain tree diversity and structure in undisturbed conditions. Regeneration of *c.* 80% of the species was found in the establishing phase (poles); the diameter structure was typical of native forests with the number of individuals decreasing with increasing size classes and showing little change over the six years; recruitment compensated for the mortality of most of the abundant species. The soils in Gama gallery forest were dystrophic with high aluminium content. Multivariate analysis suggested the stream, natural gaps and edges as the main causes of floristic differentiation at the community level.

### Introduction

The gallery forests are narrow strips of tropical forests that occur alongside the rivers in central Brazil. The dominant vegetation of the region is cerrado: savanna including several phytophysiognomies from grasslands to woodlands (Cole 1986). The soils are dystrophic and suffer from a strong seasonal variation in their soil-water regime. Soils and fire have been considered more important determinants of the vegetation in the region than the climate (Beard 1955; Coutinho 1979; Cole 1986j; Emmerich 1990). According to Beard (1955) the gallery forest would be the climatic climax of the region. The well-drained alluvial soils and constant humidity derived from the proximity of the watercourses favour these forests; fire does not normally penetrate their sharp boundaries.

The gallery forests are protected by law in Brazil (Law No. 7.511 of 7 July 1986). They are important in protecting the headwaters, controlling erosion, functioning as buffer zones and filtering chemicals (Lowrance *et al.* 1984). However, in practice, watercourses are increasingly polluted from illegal clearing of gallery forests and their subsequent erosion. Chemicals leaching from the extensive soya and other plantations in the surrounding cerrado are also polluting them. Intensive gold mining in large areas has also caused erosion and pollution from mercury poisoning.

Ecological restoration of gallery forests in Brazil is very difficult since only a few surveys exist (see UFPR/FZDF 1992; Ratter *et al.* 1973; Ratter 1980; Pereira *et al.* 1988; Heringer & Paula 1989; Oliveira-Filho *et al.* 1990; Paula *et al.* 1990; Seabra *et al.* 1991;

Felfili & Silva Junior 1992). This detailed synecological study of the Gama gallery forest is one step towards understanding the structure and function of gallery forest ecosystems.

## Materials and methods

### *Study site*

This study was carried out in 64 ha of the Gama gallery forest in the Fazenda Agua Limpa (15° 56' - 15° 59' S and 47° 55' - 47° 58' W), Federal District in Brazil. The Fazenda Agua Limpa is at an average altitude of 1100 m and contains several physiognomies of the cerrado, being very representative of central Brazilian vegetation. As in all the Federal District, the cerrado *sensu stricto*, a tree and scrub woodland, is the predominant vegetation type. The gallery forests occur around the Gama stream and two tributaries rising in the area, the Capetinga and the Olho d'gua da Onça streams. The cerrado in the uplands is separated from the gallery forests by a strip of *campo limpo* (savanna grassland with few scattered trees) whose surface is seasonally saturated (Ratter 1980). The Gama e Capetinga forests occur on well drained soils. According to the Köppen classification, the climate is Aw. The mean annual temperature is around 20.4 °C and the monthly oscillation is on average 3.3 °C. The maximum average temperature is 28.5 °C and the minimum average 12.0 °C. The relative humidity between May and September is below 70%; the minimum humidity occurs in August with an average of 47% but may fall to 15%. The daily variability is very wide, particularly in September. The average annual precipitation is 1600 mm with a coefficient of variability around 15%. Rainy summers and drier winters are typical. The rainy season starts in September, reaching a maximum in November of 270 mm, the minimum occurring between June and August (Nimer 1989).

### *Continuous inventory*

The systematic design adopted in the current work was the continuous strip layout (Loetch & Haller 1974). There were 151 (10×20 m) permanent plots lying continuously along ten transects. These were placed at right angles to the Gama stream and 100 m equidistant from each other, see Fig. 1.

The total sample was 3.02 ha and all trees from 31 cm girth (c. 10 cm diameter) at breast height (gbh)

were labelled, identified and measured. The natural regeneration was classified according to the stage of development of the young individuals. Those were sampled in subplots of different sizes within the (10 m×20 m) permanent plots: seedlings ( $H < 1$  m) in 2×2 m subplots, saplings ( $1 \text{ m} \leq H$  &  $\text{gbh} < 16$  cm) in 5×5 m subplots, and poles ( $16 \leq \text{gbh} < 31$  cm) in 10×10 m subplots. A metre rule was used to measure the seedling height (H). A five-metre pole, a 30 m telescopic pole and a Haga gauge were used to measure height of saplings, poles and trees. Girth was measured with a girth tape to the nearest 1 mm. The measurement point at the gbh was marked with bright yellow oil paint. At the first measurement, the individuals were given a sequential label containing the transect number, the plot number and the tree number, and their X,Y coordinates were registered.

The trees were classified according to crown position and bole shape. The size of natural treefall gaps was measured in all plots. The presence of grasses, bamboos, ferns, lianas, topographic features and any indicator of disturbances was also recorded. Vouchers were collected for identification and incorporated in the Herbarium of the IBGE Ecological Reserve.

The first measurement was conducted in 1985 and repeated at three-yearly intervals. This paper is based on the measurement of individuals during the period 1985–1991. The complete list of species and authorities by families, considering all individuals from 16 cm gbh (c. 5 cm diameter) is already published (Felfili & Silva Junior 1992).

### *Soil analyses*

In September 1989, one year after the second vegetation survey, two of the ten transects were selected for soil sampling (see Fig. 1). The idea was to have one sample in the first half of the study-area and another in the second. One transect was chosen randomly within the first group of five transects and another in the second group. Transect 4 is 280 m long with 14 plots (10 m×20m each) sampled in the vegetation survey. Soil profiles were described in plots 1, 5 and 14 and in the campo limpo area, next to plot 14. Transect 9 is 640 m long with 32 plots sampled in the vegetation survey. Soil profiles were described in plots 2, 6 and 15 and in the campo limpo next to plot 32.

The description of the profiles was made with the assistance of Dr M. Haridasan, soil scientist at the University of Brasilia. The natural variation in the soil determined the depth of each layer at each profile.

Soil samples were collected from different depths in each profile for laboratory analysis. Soil texture was determined by Bouyoucos's method and organic carbon by Walkley's method. Soil pH was measured in 1:2.5 soilwater suspension and in 1N KCl. Available Ca, Mg and Al were determined in soil extracts of 1N KCl. Available K, P, Fe, Mn, Zn and Cu were determined in soil extracts of a diacid mixture (0.05N HCl + 0.025N H<sub>2</sub>SO<sub>4</sub>) (Allen 1974).

### *Multivariate analyses*

Ecological species groups were derived from interpretation of the TWINSPAN (Hill 1979b) synthesis table. Species distribution patterns were related to the ecological classification of the individual plots. The presence of a species within an ecological site unit was compared with its average presence over all plots (Spies & Barnes 1985; Host & Pregitzer 1991).

The distribution of species and samples in the ordination space given by DECORANA (Hill 1979a) was used to identify clusters of species and to corroborate the groups derived from TWINSPAN.

## Results

### *Soil analyses*

Soil profile descriptions are given in Table 1. All profiles showed dark colours at all depths. Profile 9.15 was gravelly and had iron concretions from 30 cm. It had a lateritic layer from 30 cm as did the campo limpo profile 9.CL next to this transect. The fine roots were common down to 70 cm; they were abundant to only 16 cm in the campo limpo, while in the gallery forest they were abundant to 30–55 cm depending on the profile. The sand content, which ranged from 52.4 to 11.4% in the first layer, was higher for the gallery forest profiles closer to the stream and decreased towards the campo limpo. There was very little variation with either site or soil depth in the chemical composition of soils. The complete description of the results is given in Felfili (1993). The soil pH (H<sub>2</sub>O) was strongly acidic (4.4) in the first layer of transect 4 profiles, increasing with depth. Along transect 9 soil pH was higher than in transect 4, from 4.8 to 5.0. The highest value was found in the campo limpo 9 CL next to transect 9.

The organic carbon content %C decreased with depth in all profiles and from the streamside towards the campo limpo. Profile 4.5 on transect 4 had the

highest values (7.01% in the first depth). Phosphorus was low, transect 9, from 4.2 to 11.2 µg/g had higher values than transect 4. But, profile 9.15, which had the lateritic concretions, had trace values from the second depth. The campo limpo profiles had similar values to their neighbouring transects.

The content of macronutrients was low in the forest and decreased with depth. The highest values were found in transect 9 profile 9.15 (0.448 meq./100 g K, 1.472 meq./100 g Ca and 0.592 meq./100 g Mg). This profile (9.15) showed a much higher content of Ca than the others which ranged from 0.083 to 0.74 meq./100 g. The campo limpo following this profile also showed an abnormally high content of Ca. Micronutrient contents were also low, with the highest values (155.20 µg/g Fe, 4.02 µg/g Zn and 1.48 µg/g Cu) found in the campo limpo. The Zn decreased with depth in all profiles.

The Al showed toxic levels for cultivated plants, saturation ranging from 59 to 95% at the first depth of the gallery forest profiles. In the profiles along transect 9, the soils had lower Al content while pH, organic C, P and Ca contents were higher.

### *Multivariate analyses*

The TWINSPAN classification analyses for the most abundant species (those with more than 10 trees/ha see Table 2) suggest that some of them had a more restricted distribution, such as *Metrodorea pubescens*, *Cheilochlinium cognatum*, *Protium brasiliense* and *Lamanonia tomentosa*, while others were widespread in the forest such as *Licania apetala*, *Amaioua guianensis*, *Gutteria sellowiana* and *Cryptocarya aschersohniana*.

The first axis of the DECORANA ordination of all plots, shows a continuum. Most plots were between 1 SD (unit of distance along the gradient called 'average standard deviation of species turnover') and 2.5 SD. It gives high SD values for plots away from the stream, on the left side of the TWINSPAN division, and low for streambank ones (those up to 20 m around the streambed), on the right side of the division. The second axis gives lower values for plots located on naturally disturbed sites (those in gaps with a canopy opening of 4 m<sup>2</sup> or more, or in the forest edges), see Fig. 2.

The positioning of the plots on transects four and nine (see Fig. 3), do not indicate any clear pattern; the small difference in soil fertility found in those sites seems insufficient to determine changes in the vegetation.

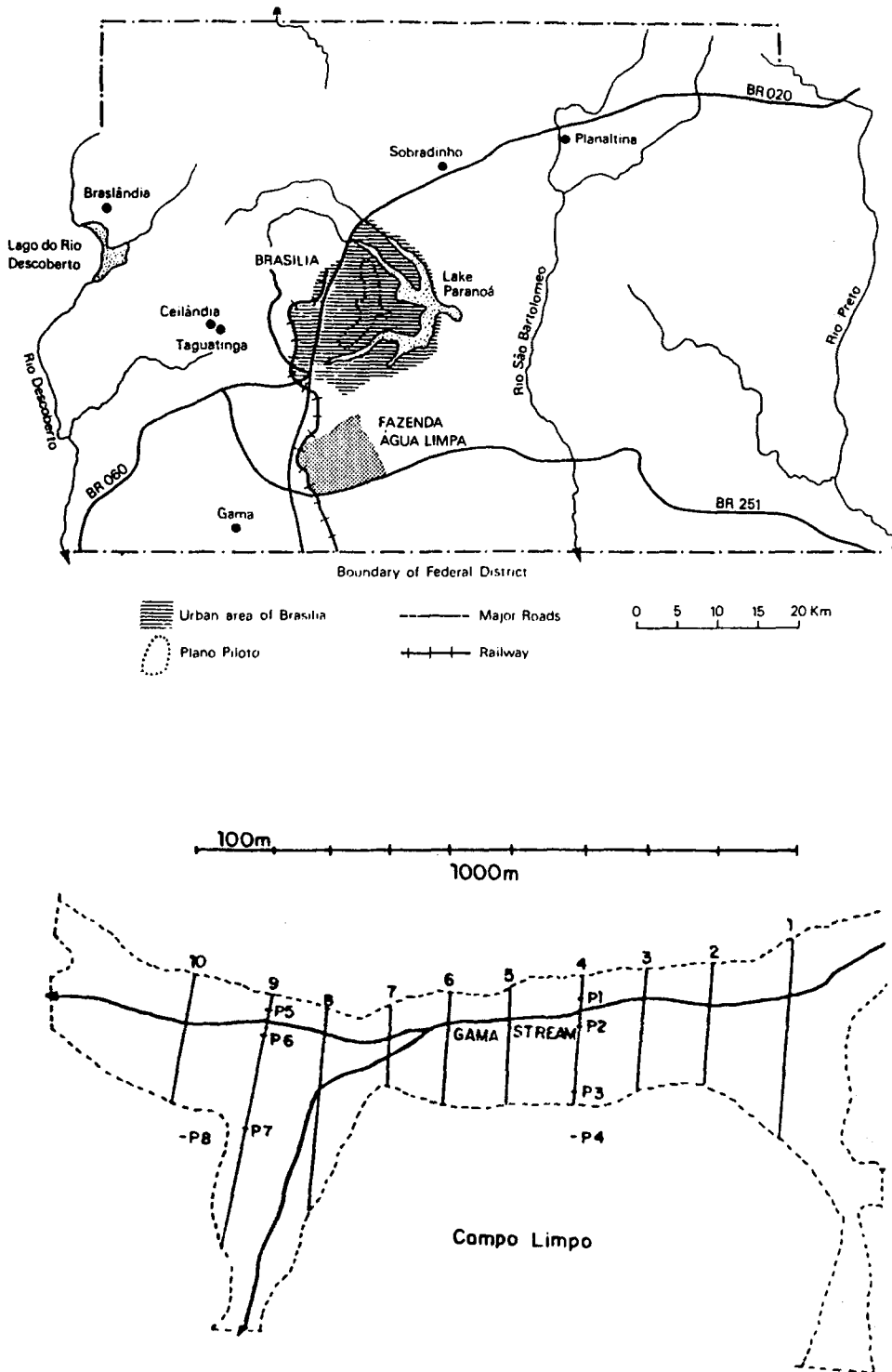


Fig. 1. Location of Fazenda Agua Limpa, Federal District, Brazil and systematic design in Gama gallery forest (transects: 1 to 10, soil profiles: p1 to p8, CL=campo limpo).

Table 1. Soil profile descriptions for the Gama gallery forest in the Fazenda Agua Limpa, Federal District, Brazil.

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<b>Site: Gallery Forest Line 4</b>	
<i>Profile 4.1</i>	
0–12 cm,	5 YR 2.5/2 moist, dark reddish brown; clay; weak very small to small crumbs; slightly sticky and very plastic; clear smooth boundary;
12–30 cm,	5 YR 3/2 moist, dark reddish brown; clay; weak very small crumbs; sticky and very plastic; clear smooth boundary.
30–70 cm,	5 YR 3/3 moist, dark reddish brown; clay; massive 'in situ' which breaks up into weak very small crumbs; sticky and very plastic; clear smooth boundary.
70–97 cm,	5 YR 3/3 moist dark reddish brown; >50% massive black material; clay; massive 'in situ' which breaks up into moderate very small crumbs; sticky and very plastic. Abundant very fine roots up to 30 cm; very common up to 70 cm.
<i>Profile 4.5</i>	
0–8 cm,	10 YR 2/1 moist, black; clay; strong very small to small crumbs; sticky and very plastic; clear smooth boundary.
8–20 cm,	10 YR 2/1 moist, black; clay; weak moderate crumbs which /breaks up into strong very small crumbs; slightly sticky and very plastic; clear smooth boundary.
20–100 cm,	10 YR 2/1, black; clay; massive 'in situ' which breaks up into strong very small crumbs; slightly sticky and very plastic. Abundant very fine roots up to 45 cm.
<i>Profile 4.14</i>	
0–12 m,	5 YR 2/2 moist, dark reddish brown; clay; moderate to strong very small to small crumbs; slightly sticky and very plastic; clear smooth boundary.
12–43 cm,	7.5 YR 3/2 moist, dark brown; clay; weak small to moderate subangular blocky which breaks up into moderate very small crumbs; slightly sticky and very plastic; diffuse smooth boundary.
43–90+ cm,	10 YR 4/6 moist, dark yellowish brown; clay; massive 'in situ' which breaks up into very weak small to moderate subangular blocky; very sticky and very plastic. Abundant very fine roots up to 43 cm; few up to 90 cm.
<b>Site: Campo limpo Line 4</b>	
<i>Profile 4.CL</i>	
0–16 cm,	7.5 YR 3/2 moist, dark brown; clay; strong small crumbs; slightly sticky and very plastic; clear smooth boundary.
16–31 cm,	7.5 YR 4/4 moist, dark brown; clay; the weak moderate subangular blocky which breaks up into moderate small crumbs; slightly sticky and very plastic; clear smooth boundary.
31–54 cm,	7.5 YR 4/6 moist; strong brown, clay; massive 'in situ'; very sticky and very plastic; diffuse smooth boundary.
54–70 cm,	YR 5/6 moist, strong brown, clay, massive 'in situ'; very sticky and very plastic; diffuse smooth boundary.
70–100+ cm,	7.5 YR 5/8 moist, strong brown, clay, massive 'in situ' very sticky and very plastic. Abundant very fine roots up to 16 cm, common up to 70 cm.
<b>Site: Gallery forest Line 9</b>	
<i>Profile 9.2</i>	
0–8 cm,	10 YR 2/2 moist, dark yellowish brown; clay; moderate very small to small crumbs; slightly sticky and slightly plastic; clear smooth boundary.
8–32 cm,	10 YR 2/1 moist; black; clay; weak small subangular blocky; slightly sticky and slightly plastic; diffuse smooth boundary.
32–100+ cm,	10 YR 2/2 moist, very dark brown; clay; massive 'in situ'; slightly sticky and slightly plastic. Abundant fine roots up to 55 cm.

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The first axis of the DECORANA ordination for all species also shows a continuum, as shown by Fig. 4. It gives high SD values for preferential species of 'dry' sites such as *Aspidosperma olivaceum* and *Metrodorea pubescens*, and low values for preferential species of 'wet' sites such as *Calophyllum brasiliense* and *Protium brasiliense*. The second axis also gave low SD values for preferential species of naturally disturbed sites such as *Piptocarpha macropoda* and *Sclerolobi-*

*um paniculatum*. Widespread species, such as *Licania apetala* and *Amaioua guianensis* had intermediate values.

#### *Floristic composition and diversity*

In 1985, 1,962 individuals with gbh equal to or greater than 31 cm were measured in the Gama gallery forest. They belonged to 44 families, 75 genera and 87

Table 1. Continued.

<i>Profile 9.6</i>	
0–20 cm,	10 YR 2/2 moist, very dark brown.; clay; weak very small crumbs; slightly sticky and slightly plastic; diffuse smooth boundary.
20–55 cm	10 YR 3/2 moist, very dark greyish brown; clay; massive 'in situ', which breaks up into weak moderate subangular blocky; sticky and plastic; diffuse smooth boundary.
55–100+ cm,	10 YR 3/3 moist; dark brown; clay; massive 'in situ' which breaks up into weak moderate subangular blocky; sticky and very plastic. Abundant fine roots up to 55 cm.
<i>Profile 9.15</i>	
0–17 cm,	10 YR 2/2 moist; very dark brown; gravelly; clay; weak very small crumbs; slightly sticky and slightly plastic; gradual smooth boundary.
17–35 cm:	10 YR 3/2 moist; very dark greyish brown; gravelly; clay; small weak crumbs; slightly sticky and slightly plastic; gradual smooth boundary.
30–70+ cm,	10 YR 4/3 moist; dark brown; iron concretions, gravelly; clay; sticky and plastic. Abundant fine roots up to 30 cm.
<b>Site: Campo Limpo Line 9</b>	
<i>Profile 9.CL</i>	
0–5 cm,	gravelly (>80%), clear smooth boundary
5+ cm,	massive plinthite layer.

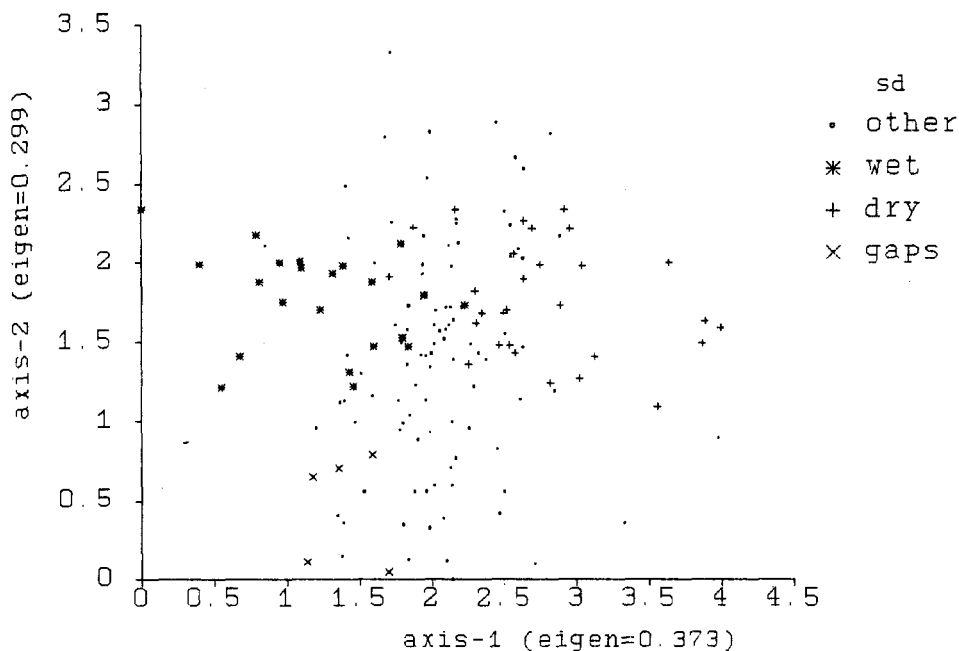


Fig. 2. DECORANA ordination for plots in Gama gallery forest, Federal District, Brazil. Axis scales are in units of average standard deviations of species turnover.

species plus five species only determined at family level and one undetermined, totalling *c.* 81 genera and 93 species. Shannon's diversity index ( $H'$ ) was 3.84 and Pielou's evenness index ( $J'$ ) was 0.84. All the species found in 1985 were also found in the following measurements (1988 and 1991) plus three new species.

Individuals of five species that occur as trees in other gallery forests, plus two other species that did not reach 31 cm gbh, were only found under 31 cm gbh (Felfilli & Silva Junior 1992). More than 90% of the species from 31 cm gbh were also among the natural regeneration. For example, 82 of those species also

Table 2. Density and basal area of trees from 31 cm girth in 1985 and poles (individuals between 16 cm and 31 cm gbh) in the Gama gallery forest in Fazenda Agua Limpa, Federal District, Brazil.

Species <sup>a</sup>	Trees <sup>b</sup>				Poles <sup>b</sup>			
	Density		Basal area		Density		Basal area	
	n/ha	%	m <sup>2</sup> /ha	%	n/ha	%	m <sup>2</sup> /ha	%
<i>Lamanonia tomentosa</i>	31.13	4.79	3.246	10.67	0.68	0.11	0.002	0.06
<i>Copaifera langsdorffii</i>	24.50	3.77	2.477	8.14	4.05	0.65	0.019	0.79
<i>Aspidosperma olivaceum</i>	30.13	4.64	1.982	6.52	5.41	0.87	0.024	1.03
<i>Metrodorea pubescens</i>	38.41	5.91	1.321	4.34	36.49	5.86	0.129	5.38
<i>Amaioua guaianensis</i>	37.09	5.71	0.800	2.63	65.54	10.52	0.267	11.16
<i>Licania apetala</i>	33.11	5.30	1.143	3.76	24.32	3.90	0.113	4.72
<i>Guatteria sellowiana</i>	34.11	5.25	0.949	3.12	18.24	2.93	0.076	3.22
<i>Nectandra mollis</i>	24.17	3.72	1.496	4.92	4.73	0.76	0.019	0.81
<i>Tapirira guianensis</i>	23.51	3.62	1.338	4.40	29.05	4.66	0.118	4.92
<i>Probum brasiliense</i>	28.15	4.33	1.052	3.46	26.35	4.23	0.111	4.64
<i>Cheiloclinium cognatum</i>	33.11	5.10	0.543	1.79	29.73	4.77	0.122	5.10
<i>Piptocarpha macropoda</i>	27.48	4.23	0.644	2.12	14.19	2.28	0.057	2.37
<i>Callisthene major</i>	14.24	2.19	1.486	4.89	1.35	0.22	0.007	0.30
<i>Cryptocarya aschersoniana</i>	16.56	2.55	1.087	3.57	12.16	1.95	0.046	1.95
<i>Maytenus alaternoides</i>	16.23	2.50	0.256	0.84	28.38	4.56	0.120	5.02
<i>Emmotum nitens</i>	11.92	1.83	0.547	1.80	3.38	0.54	0.012	0.50
<i>Machaerium acutifolium</i>	8.61	1.33	0.470	1.55	5.41	0.87	0.017	0.70
<i>Cupania vernalis</i>	11.26	1.73	0.290	0.95	4.05	0.65	0.014	0.58
<i>Ouratea castaneaefolia</i>	11.59	1.78	0.269	0.89	16.22	2.60	0.061	2.54
<i>Matayba guianensis</i>	9.60	1.48	0.265	0.87	12.16	1.95	0.046	1.94
<i>Qualea multiflora</i>	4.30	0.66	0.741	2.44	3.38	0.54	0.011	0.47
<i>Myrsine coriacea</i>	6.29	0.97	0.509	1.67	1.35	0.22	0.005	0.23
<i>Cabralea canjerana</i>	5.63	0.87	0.436	1.43	6.08	0.98	0.018	0.76
<i>Saccoglottis guidaensis</i>	6.62	1.02	0.294	0.97	2.03	0.33	0.009	0.37
<i>Maprounea guianensis</i>	5.63	0.87	0.418	1.37	2.03	0.33	0.007	0.29
<i>Roupala montana</i>	6.95	1.07	0.205	0.67	2.03	0.33	0.008	0.34
<i>Terminalia brasiliensis</i>	2.65	0.41	0.636	2.09	2.03	0.33	0.007	0.30
Others	146.69	22.60	5.52	18.14	262.14	42.06	0.945	39.51
Total	649.67	100	30.42	100	622.96	100	2.39	100

<sup>a</sup> There were a total of 93 trees species and 87 poles, five species among the poles were not found as trees, only the most abundant species are listed here in decreasing order of density.

<sup>b</sup> Confidence intervals (95%) for trees: Density [620 - 679]; Basal area [28.2 - 32.6] and for poles: Density [573 - 673]; Basal area [2.19 - 2.58].

occurred as poles (individuals from 16 cm to 31 cm gbh), indicating a self-regenerating community.

The predominant families in number of species were Leguminosae (9), Myrtaceae (8), Rubiaceae (6), Lauraceae (4), Apocynaceae (4), Melastomataceae (4), Vochysiaceae (4), Annonaceae (3), Guttiferae (3), Moraceae (3) and Sapotaceae (3). These 11 families had approximately 50% of the total number of species. Only seven families, Annonaceae, Apocynaceae, Melastomataceae, Myrtaceae, Combretaceae, Ochnaceae and Vochysiaceae had more than

one species per genera. The richest genera in number of species were *Aspidosperma*, *Miconia* and *Myrcia*.

The species-area curve levels off, as seen in Fig. 5, before the first 1.5 ha. This proves that the sampling was sufficient to represent the floristic composition of the forest (Mueller-Dombois & Ellenberg 1974). The curve for the 3.01 ha sample is in Felgili (1993).

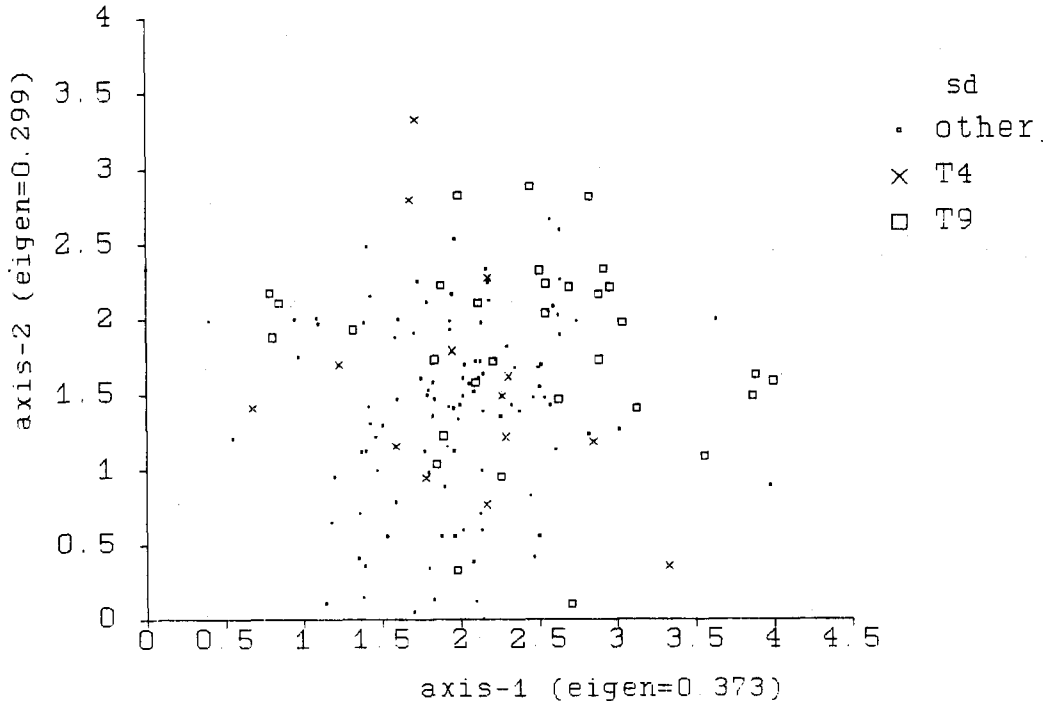


Fig. 3. DECORANA ordination for plots in Gama gallery forest, Federal District, Brazil. T4, T9 = plots on transect 4 and 9. Axis scales are in units of average standard deviations of species turnover.

### Community structure

In the first measurement, in 1985, only living trees were recorded and there were 649 trees/ha with a basal area of 30.40 m<sup>2</sup>/ha. There was a reduction of 2% in the number of living individuals and 3% in basal area of the forest over the next six years. Standing dead trees represented around 3% of the total density.

This forest was characterized by many species occurring at low density. In 1985 for example, only 18 species were abundant with at least ten trees/ha (see Table 2), while 21 species were rare with less than one tree/ha. The majority (53 species) occurred at intermediate density between one and ten trees/ha. The most abundant species, *Amaioua guianensis*, contained less than 7% of the total number of individuals.

The diameter distribution of all trees and species combined (from 10 cm diameter) showed a reversed-J shape. Their changes over time were not significant by Kolmogorov-Smirnov test at 10% level. The forest was composed mainly of species with small individuals, with a maximum diameter of 45 cm for 90% of the individuals and 85% of the species.

The height distribution of trees from 10 cm dbh was a bell-shaped curve. The lowest trees were between 2

and 6 m high, while the tallest reached from 24 to 28 m. and, most of the population were between 12 and 20 m high. The distribution of all heights from 5 m high, which included natural regeneration, showed a higher concentration of individuals in the smaller classes.

### Community dynamics

The mean annual diameter increment for the community, considering all species and all individuals above 10 cm diameter (from 1985 to 1991) was 0.25 cm/year. Median values were lower, c. 0.18 cm/year. The periodic mean annual increments and variability coefficients (cvs) by species are also shown in Table 3 for the most abundant species.

The mortality in the Gama community for this period, was 19% (3.5%/year) based on a logarithmic model (Lieberman & Lieberman 1987). Recruitment was 16% for this period. Periodic mean annual rate was 2.67%. Approximately 86% of all species recorded over the six-year period either suffered mortality or gained recruits or both.

From 1985 to 1991, 67 species gained recruits while 69 suffered mortality. For the same period, the difference between mortality and recruitment was zero



Table 3. Periodic mean diameter increment and variability coefficients (cvs) per species in the Gama gallery forest in Fazenda Agua Limpa, Federal District, Brazil.

Species*	n	1985–1988 <sup>a</sup>		1988–1991 <sup>b</sup>		1985–1991 <sup>c</sup>	
		pmai cm	cv%	pmai cm	cv%	pmai cm	cv%
<b>Species above mean (mean increment <math>\geq 0.25</math> cm/year)</b>							
<i>Metrodorea pubescens</i>	103	0.28	143	0.22	95	0.25	95
<i>Lamanonia tomentosa</i>	82	0.25	140	0.29	160	0.28	161
<i>Protium brasiliense</i>	76	0.33	71	0.25	76	0.29	76
<i>Copaifera langsdorfii</i>	70	0.31	87	0.23	65	0.26	65
<i>Nectandra mollis</i>	67	0.31	81	0.31	114	0.30	114
<i>Tapirira guianensis</i>	61	0.43	79	0.37	74	0.39	74
<i>Piptocarpha macropoda</i>	51	0.37	104	0.54	80	0.47	80
<i>Cryptocarya aschersoniana</i>	44	0.35	87	0.29	81	0.32	81
<i>Callisthene major</i>	39	0.31	104	0.21	81	0.27	81
<i>Emmotum nitens</i>	29	0.33	89	0.23	75	0.26	75
<i>Machaerium acutifolium</i>	21	0.25	118	0.16	86	0.21	86
<i>Micropholis venulosa</i>	18	0.42	91	0.20	91	0.34	67
<i>Myrsine coriacea</i>	17	0.35	134	0.41	140	0.40	134
<i>Sclerobium paniculatum</i>	12	0.72	74	0.72	82	0.71	82
<i>Virola sebifera</i>	12	0.28	62	0.17	49	0.22	49
<i>Apuleia mollaris</i>	11	0.30	94	0.28		0.29	81
<i>Inga alba</i>	11	0.27	116	0.31	73	0.23	73
<i>Ixora warmingii</i>	11	0.42	90	0.15	64	0.28	64
<i>Pouteria ramiflora</i>	10	0.34	80	0.14	75	0.23	75
<b>Species below mean (mean increment <math>&lt; 0.25</math> cm/year)</b>							
<i>Amaioua guianensis</i>	102	0.18	113	0.24	132	0.22	132
<i>Licania apetala</i>	88	0.19	104	0.15	73	0.16	73
<i>Guatteria sellowiana</i>	88	0.15	128	0.23	111	0.17	111
<i>Cheilochlinium cognatum</i>	86	0.15	103	0.14	99	0.15	99
<i>Aspidosperma olivaceum</i>	78	0.31	80	0.13	71	0.22	71
<i>Maytenus alaternoides</i>	40	0.13	102	0.16	86	0.14	86
<i>Ouratea castaneaefolia</i>	34	0.22	172	0.15	122	0.16	122
<i>Matayba guianensis</i>	28	0.20	100	0.20	93	0.21	93
<i>Cupania vernalis</i>	25	0.23	107	0.12	101	0.15	101
<i>Saccoglottis guianensis</i>	18	0.18	131	0.08	135	0.13	136

for 55 species (66%), between  $-5$  and  $+5$  for 20 species (24%), and between  $-10$  and  $+10$  for five species (6.0%). Only three species showed changes greater than that, being the most dynamic species. *Amaioua guianensis* gained 17 trees over the six years, representing an increase of 17% over the original population in 1985. However, *Lamanonia tomentosa* lost 13 trees (a reduction of 15%) and *Piptocarpha macropoda* lost 32 (a reduction of 40%).

Among the other species that suffered losses, the highest were *Aspidosperma olivaceum* ( $-5$ ), *Qualea multiflora* ( $-5$ ), *Nectandra mollis* ( $-7$ ) and *Emmotum*

*nitens* ( $-9$ ) while *Gomidesia lindeniana* ( $+6$ ), *Cheilochlinium cognatum* ( $+8$ ), *Inga alba* ( $+8$ ) and *Ouratea castaneaefolia* ( $+10$ ) were among those that gained more trees.

There was a significant relationship ( $p < 0.0001$ ) between density and mortality ( $r = 0.64$ ;  $n = 83$ ) and density and recruitment ( $r = 0.72$ ;  $n = 83$ ) of species. There was also a significant relationship ( $p < 0.0001$ ) between density of adult trees ( $\geq 10$  cm dbh) and density of poles (5 cm–10 cm dbh) of the same species ( $r = 0.74$ ;  $n = 82$ ).

Table 3. Continued.

Species*	n	1985–1988 <sup>a</sup>		1988–1991 <sup>b</sup>		1985–1991 <sup>c</sup>	
		pmai		pmai		pmai	
		cm	cv%	cm	cv%	cm	cv%
Leguminosae indet.	15	0.14	155	0.08	117	0.09	117
<i>Myrcia eriopus</i>	15	0.20	115	0.13	93	0.16	93
<i>Cabralea canjerana</i>	14	0.19	148	0.16	114	0.19	114
<i>Maprounea guianensis</i>	14	0.23	67	0.22	80	0.19	80
<i>Roupala montana</i>	14	0.10	90	0.11	—	0.10	—
<i>Aspidosperma cylindrocarpon</i>	13	0.16	189	0.07	140	0.06	140
<i>Salacia elliptica</i>	13	0.16	137	0.37	77	0.27	77
<i>Aspidosperma</i> sp.	12	0.21	153	0.13	97	0.23	153
<i>Aspidosperma subincanum</i>	10	0.23	96	0.22	71	0.23	79

<sup>a</sup> Mean annual increment for the whole forest = 0.26 cm, Median 0.20 cm, cv = 111%,  $CI_{p(0.95)}$  = [0.25 cm - 0.27 cm], n = 1667 (period 1985–1988).

<sup>b</sup> Mean = 0.24 cm, Median = 0.16 cm, cv = 158%,  $CI_{p(0.95)}$  = [0.20 cm - 0.26 cm], n = 1517 (period 1988–1991).

<sup>c</sup> Mean = 0.25 cm, Median = 0.18 cm, cv = 136%,  $CI_{p(0.95)}$  = [0.23 cm - 0.27 cm], n = 1517 (period 1985–1991).

\* Only species with 10 or more individuals were listed in this table but the community means and medians included all species and individuals; pmai = periodic mean annual increment, n = number of sampled trees, cv = Variability coefficient, CI = confidence interval.

Table 4. Minimum diameter, number of sampled trees, tree density/ha and basal area/ha in some sites in several Brazilian vegetation types.

Site	Source	Minimum diameter (cm)	Number of sampled trees	Density	Basal area (m <sup>2</sup> /ha)
Forest					
Gama gallery	Present study	10	1,960	649	30.40
Gelado Amazonia	Silva <i>et al.</i> 1987	10	516	516	17.63
Camaipi Amazonia	Mori <i>et al.</i> 1989	10	546	546	35.10
BR 364 Amazonia	Salomao & Lisboa 1988	10	573	573	31.05
Carajás Amazonia	Salomao <i>et al.</i> 1988	10	483	483	21.58
Juruá Amazonia	Campbell <i>et al.</i> 1992	10	523	523	25.46
Juruá Amazonia	Campbell <i>et al.</i> 1992	10	420	420	27.01
Juruá Amazonia	Campbell <i>et al.</i> 1992	10	777	777	25.72
Savanna					
Cerrado s.s.	Felfili & Silva Junior 1988	10	729	347	—
Cerrado s.s.	Felfili & Silva Junior 1992	5	2,011	958	7.34

## Discussion

### Soils and environmental determinants

The profiles closer to the stream showed black colour either at all (see profile 4.5) or some depths (see profile 9.2 second depth) suggesting poor drainage. The

influence of the fluctuations of the water table close to the surface is seen in the greyish layers in profiles 9.6 and 9.15. And also in the reddish and yellowish stains found in profiles 4.1, 4.14 and 9.6. According to EMBRAPA (1978) these soils originate from sedimentary deposits from the Quaternary. The grey colour in

the horizon is characteristic of the iron reduction in the hydromorphic gley soils.

The organic carbon content of Gama gallery forest soil was intermediate between cerrado s.s. sites with an average of 2.7% (Furley 1985) and a semideciduous forest on mesotrophic soils in the same region with an average of 13% (Ramos 1989).

The soils under gallery forests in central Brazil have been little studied and the general belief has been that they are hydromorphic or alluvial soils (EMBRAPA 1978) and more fertile (Ribeiro *et al.* 1983) than the surrounding latosols, cambisols and others covered by the cerrado physiognomies, the dominant vegetation in the region. However, more recent studies, including this study, show that different soil units can be found under the gallery forest. The soils can also be as poor in nutrients as the cerrado soils (Cavedon & Sommer 1990; Silva 1991).

The success of the TWINSPAN classification can be assessed by the current knowledge of the ecology of some species. Some positive indications were: (1) The positioning of *Qualea multiflora* and *Roupala montana*, species common to gallery forests and cerrado in the region (Ratter 1980; Felfili & Silva Junior 1992) at the 'dry' association; (2) Light demanding species such as *Cecropia pachystachya* and *Piptocarpha macropoda* and species common with cerrado such as *Emmottum nitens*, *Qualea dichotoma* and *Sclerolobium paniculatum* (Ratter 1980; Felfili & Silva Junior 1992) were grouped in the 'gaps' association, whose sites receive extra light; (3) The presence of *Protium brasiliense*, *Pseudolmedia laevigata* and *Calophyllum brasiliense*, commonly found alongside streams in the region and in swampy gallery forest (Ratter 1980; Silva 1991) in the 'wet' association.

The adaptation of the plants for avoiding some toxic elements, for exploiting scarce nutrient resources in the poor soils, through their efficiency in absorbing them or having low requirements, is certainly an important mechanism in determining the patterns of vegetation in the cerrado region. The results of the present study suggest that nutrients were not the main determinants in the occurrence of gallery forest on the dystrophic soils of the Fazenda Agua Limpa-DF. And, multivariate analyses indicate that there is variation in the floristic composition of plots in relation to moisture and disturbance gradients. Detailed studies on the role of soil humidity, physical structure, geomorphology, nutrient cycling and other aspects of plant-soil relationships would be required for a better understanding of the vegetation-soil relationships in central Brazil.

#### Floristic composition and diversity

The major families found in Gama forest were also among the major families found in other gallery forests in Fazenda Agua Limpa (Ratter 1980; Felfili & Silva Junior 1992). Leguminosae and Myrtaceae were considered the most important families in the Federal District Inventory of forestry resources (UFPR/FZDF 1972). Annonaceae and Melastomataceae were abundant mainly in damp areas in gallery forests of the Federal District and Sao Paulo (Ratter 1980; Bertoni & Martins 1987). Methodological differences, mainly sampling size and minimum diameter, make comparisons of diversity indices in different sites difficult (Margurran 1988). However, a Shannon's index of 3.84 found for this forest can be considered high. It is in the range of those found for Atlantic and Amazonian rainforests in Brazil, from 3.7 to 4.3 for trees from 10 cm dbh (Silva & Leitao Filho 1982). It was higher than those found for cerrado s.s. in central Brazil, from 3.11 to 3.62 (Felfili & Silva Junior 1993) and for the neighbouring cerrado s.s. (3.46) and cerrado (3.42) in Fazenda Agua Limpa (Felfili & Silva Junior 1992), both for trees from 5 cm diameter.

Comparing the species-area curves in Fig. 5, the cerrado s.s. site (Felfili & Silva Junior 1992) had more species in the first 1,000 m<sup>2</sup>. The Gama and the Amazonian terra firme forest site (Rodrigues 1963) were similar initially. However, the cerrado s.s. curve levelled off first with 62 species in 1.5 ha while the Amazonian sites curves did not stabilize with 96 species. This gallery forest was intermediate, levelling off with 82 species in 1.5 ha.

#### Community structure

The density and basal area of this forest are near those found in several Brazilian forest formations. They are twice as high as that found for the cerrado s.s. in Fazenda Agua Limpa, see Table 4.

*Lamanonia tomentosa* followed by *Copaifera langsdorffii*, *Metrodorea pubescens*, *Amaioua guianensis*, *Aspidosperma olivaceum*, *Licania apetala*, *Guatteria sellowiana*, *Tapirira guianensis*, *Nectandra mollis*, *Protium brasiliense*, *Cheiloclinium cognatum*, *Piptocarpha macropoda*, *Callisthene major* and *Cryptocarya aschersoniana* had more than 50% of the total density and basal area in all occasions (see Table 2). These species can be considered the most successful in exploiting the habitat resources.

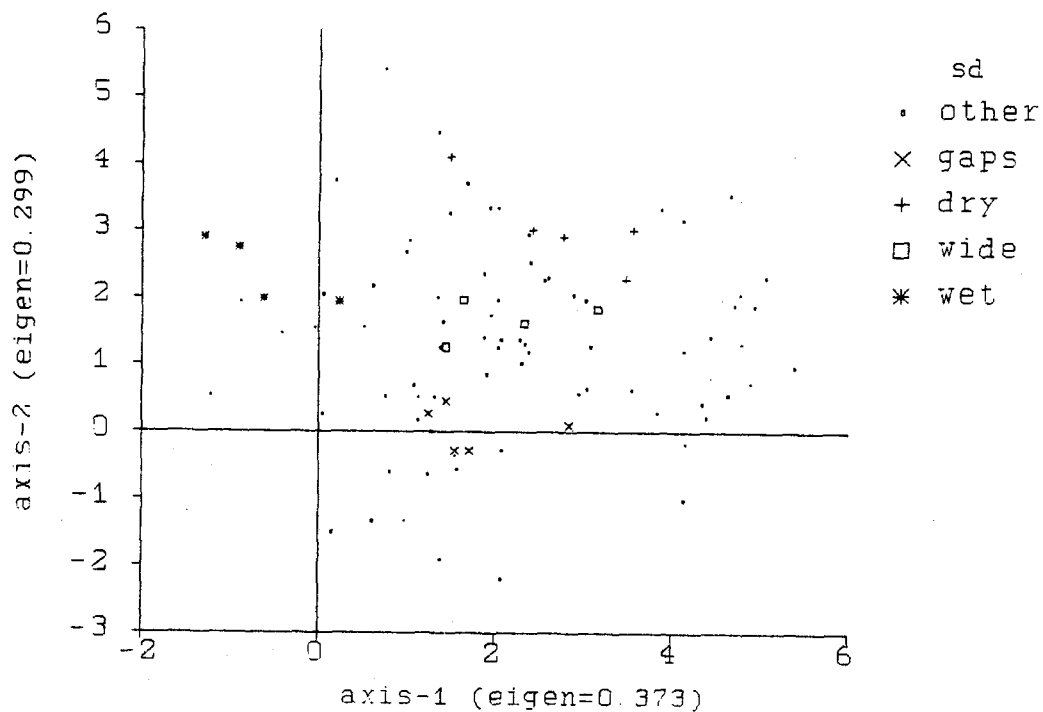


Fig. 4. DECORANA ordination for species in Gama gallery forest, Federal District, Brazil. Axis scales are in units of average standard deviations of species turnover.

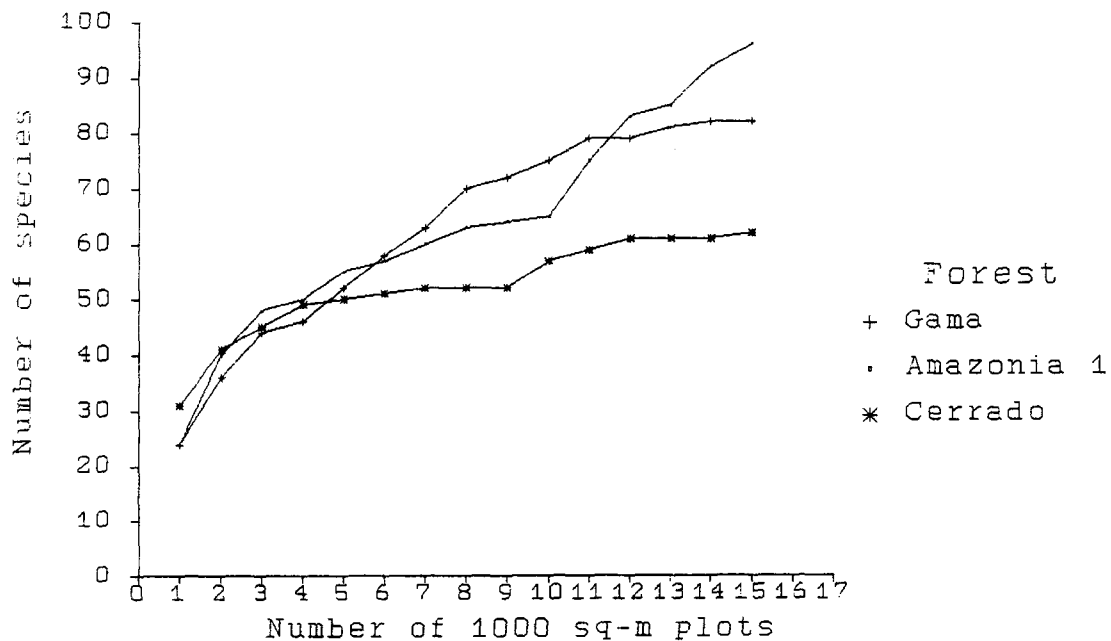


Fig. 5. Comparison of Gama gallery forest species-area curve to a cerrado s.s. and an Amazonian site, same sample size, minimum diameter 10 cm for Gama and Amazonian site and 5 cm for cerrado *sensu stricto*.

Short-lived pioneers and gap-colonizer species, such as *Cecropia pachystachya* (*Piptocarpha macropoda*), *Didymopanax morototoni*, *Sloanea* sp., *Sorocea ilicifolia*, *Cordia sellowiana* and *Pseudolmedia laevigata*) represented less than 10% of the total tree flora and occurred at low density indicating undisturbed conditions. Hartshorn (1980) also found a low density of pioneers in a mature forest in Costa Rica.

The size structure was typical of a self-regenerating community where small trees represent most of the population (Whitmore 1990). Most species reached 45 cm diameter but the maximum diameter was *c.* 100 cm. Ramos (1989) also found a similar diameter structure for a dry mesophytic forest that occurs in the same region but in mesotrophic soils on limestone outcrops. On the other hand, in cerrado s.s. (the predominant woody vegetation that surrounds the gallery forests), the size range is much smaller, and most of the species and individuals are under 10 cm diameter with very few larger trees reaching *c.* 45 cm diameter (Felfili & Silva Junior 1988; Silva Junior & Silva 1988; Nascimento & Saddi 1992). Gallery forests grow in the same acidic, aluminium toxic and nutrient poor soils as the surrounding cerrado s.s.. They support a tall and species rich forest structure in spite of the poverty in nutrients.

Only a few individuals (1.01% of the total) of eleven species in seven families reached more than 60 cm diameter: *Cryptocarya aschersoniana* and *Nectandra mollis* (Lauraceae), *Copaifera langsdorffii* (Leg. Caesalpinioideae), *Callisthene major*, *Qualea dichotoma* and *Qualea multiflora* (Vochysiaceae), *Cabralea canjerana* (Meliaceae), *Lamanonia tomentosa* (Cunoniaceae), *Tapirira guianensis* (Anacardiaceae), *Terminalia argentea* and *Terminalia brasiliensis* (Combretaceae). Large emergent trees of Leguminosae, Lauraceae and Vochysiaceae species are common in the neotropics, and their ability to fix nitrogen, as shown by the Leguminosae and that of accumulating the aluminium by the Vochysiaceae (Haridasan & Araujo 1988) may be evidence that they are especially adapted to dystrophic soils.

#### *Community dynamics*

The mean increment found for this community is near that found for an undisturbed Brazilian Amazonian site studied by Carvalho (1992), of 0.20 cm/year, over an eight-year period. Species whose trees reach large dimensions tended to have higher mean increments. This agrees with the conclusions of Swaine *et al.*

(1987b), based on a review of several works on tropical forests, that larger trees have higher growth rates.

The variation between the increments was high for the community and for individual species populations with most cvs around 100% see Table 3. Silva (1989) studying an Amazonian forest site in Brazil also found cvs in the same range. Pires & Prance (1977) studying a site in Brazilian Amazonia, Swaine *et al.* (1987a) in a moist semideciduous forest in Ghana and Gentry & Terborgh (1990) in a Peruvian Amazonian site, also found the growth highly variable even within the same species population.

The high variation between the increments is a consequence of the genetic and environmental heterogeneity of the tropical forests. Each tree has its own genetic background and its unique micro habitat conditions. For the same species, in the same diameter class, some trees do not grow due to competition and other factors such as predation by herbivores and pathogens. However, others, free of competition, may grow more than the mean causing the variation.

The mortality rate (3.5%/year) was closer to the rates found in disturbed sites in similar studies elsewhere indicating a very dynamic environment. Silva (1989) found 2.8%/year for a logged over Amazonian forest and 4.7%/year when he considered only pioneers. Carvalho (1992) found 3.1%/year and 4.3% in a logged over Amazonian forest and 1.3% in a nearby undisturbed site. Light demanding showed higher mortality rates than shade tolerant species.

The annual mean mortality (3.5%) was higher than the recruitment (2.7%) in this community giving a difference of 0.8%/year in favour of mortality, based on the period 1985–91. Manokaran & Kochummen (1987) studying a Malaysian lowland dipterocarp forest found that mortality exceeded recruitment during the first ten years of the study but it was thereafter almost exactly balanced by recruitment. Several other authors, including Pires & Prance (1977) in Brazilian Amazonia, Swaine *et al.* (1987a) in Ghana, Lieberman *et al.* (1990) in Costa Rica, Gentry & Terborgh (1990) in Peruvian Amazonia, also found a small imbalance over short periods. These results are probably due to the nature of the processes, mortality occurs first giving ground to recruitment and thus, creating the imbalance over a short time span.

Most species light demanding suffered losses while shade tolerants had gains. If this tendency persists, the canopy would suffer a qualitative change with shade tolerant species becoming more common in the Gama forest.

There was a positive correlation between mortality ( $r=0.64$ ), recruitment ( $r=0.72$ ) and density of species ( $n=83$ ). These suggest that, although the abundant species are subject to higher mortality, they also have higher recruitment, thus maintaining their dominance. Hubbell & Foster (1990) also found the most abundant species regenerating the most in Barro Colorado Forest in Panamá. Rankin-de-Merona *et al.* (1990) studying a site in Brazilian Amazonia, based on two measurements over five years, found that the ten most abundant families in the first enumeration also showed the highest mortality and recruitment rates.

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